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Fungus and Bacterial Diseases of Insects as Factors in Biological Control ..... H. S. FAWCETT 327

Recent Studies on Inheritance of Quantitative Characters in Plants ..... HAROLD H. SMITH 349

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THE BOTANICAL REVIEW

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FUNGUS AND BACTERIAL DISEASES OF INSECTS AS FACTORS IN BIOLOGICAL CONTROL

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INTRODUCTION

In comparison with investigations of entomophagous parasites (insects parasitic on other insects), experimental work on entomogenous parasites (fungi or bacteria parasitic on insects) in relation to biological control has received relatively little attention. Consideration of the latter subject, except for a few microorganisms, has not gone much beyond the observational and descriptive stage, and only a small number of well-controlled experiments have been carried out. The reason for this appears to be partly that in the past period of extreme specialization this subject has become a kind of "no man's land" between the entomologist and the plant pathologist or applied mycologist.

One apparent cause for neglect of the field has been the hasty generalization that because of failures to get outstanding results with certain fungi in initial trials, the whole field has little promise of practical results. Another is probably the preoccupation of both entomologist and plant pathologist with problems which they considered more closely related to their special fields. Mycologists, however, have in the meantime done considerable descriptive work on the occurrence and morphology of these entomogenous fungi.

An attempt will be made here not to give a complete review of the literature but to discuss some of the most important contributions and to use representative examples, mostly from entomogenous fungi and bacteria on the citrus insects, these being best known to the author.

The literature on these organisms is widely scattered. For part of them, Petch has published a large number of papers, especially on taxonomic relationships of entomogenous fungi (40–57), and

many other sources are extant (2, 4–6, 19, 22, 36, 39, 68, 71). There are also comprehensive lists of fungi on insects (14, 34), and numerous references to bacteria in and on these hosts (38, 73, 74).

GENERAL CONSIDERATIONS

In biological control of insects two opposing forces of survival, as pointed out by Chapman (11, 12), come into play, namely, "biotic potential" or inherent ability of the insect to reproduce and survive, and "environmental resistance", constituting the physical and biological factors that oppose survival. For insect survival the parasitic fungi and bacteria are a part of this environmental resistance and may constitute a small or a large factor in opposing survival, depending on the degree of parasitism and the physical conditions influencing distribution and infection. The opposing forces of biotic potential and environmental resistance also operate on the fungi themselves, and the insect's resistance to infection may be a part of the environmental resistance for the fungus. Some of the factors of biological control, especially as related to entomophagous parasites of insects, have been discussed by others (62–64, 76).

Gradation of Parasitism. Entomogenous fungi are variable in their nature and relationship to their insect hosts, as are the plant pathogenic fungi to their plant hosts. In parasitism of insects as in parasitism of plants there is apparently a gradation from the strongest and most effective parasites down to those which are very weak and indirect. Among the weak and indirect parasites, occur species about which it is difficult to tell whether they are slightly parasitic or merely living upon the insects after their death. Many that are distinctly parasitic at one stage are capable of completing their reproductive stage while growing upon the insect's body after its death. It is therefore unsafe to draw conclusions about the efficiency of the entomogenous fungi as a whole from a few examples such as the chinch bug fungus, most often referred to in publications on biological control. Four categories of parasitism may be mentioned with examples:

(*a*) Some entomogenous genera, *e.g., Sorosporella* and *Empusa,* are obligate parasites and propagate only on or within the body of the live insect. As soon as the insect dies they usually form resistant resting bodies or spores which propagate again only when they come in contact with another live insect.

(*b*) Other entomogenous genera, *e.g., Aschersonia, Aegerita* and *Nectria,* are parasitic or semiparasitic whenever the spore or fungus mycelium comes in contact with the insect, and under suitable conditions may kill the insect. They may also live a saprophytic existence on the bodies of the insects after their death. Some of this second kind may kill the insect more rapidly and be more effective in epidemics than some of the obligate parasites.

(*c*) Still other entomogenous fungi may be weak parasites, dependent on a special stage or weakened condition of the insect for their infection and propagation.

(*d*) Some species of at least one genus, *Septobasidium,* appear to have a partial symbiotic relationship to certain scale insects (15). The colony as a whole appears to be protected by a covering of mycelium, although at times part of the larvae appear to be parasitized by the fungus.

A fifth category cannot be considered as parasitic at all; the members live as saprophytes on the bodies only after the insects have died. Most species of *Cladosporium* found on insects are thought to be in this class, although some may possibly be semiparasitic under certain conditions.

Conditions Influencing Effectiveness. Although a number of these parasitic entomogenous fungi under favorable conditions develop conspicuous pustules or sporulating structures after they have killed the insect by invasion of its body, this development of conspicuous evidence of their presence may be arrested by drying conditions after infection, so that the insect body is desiccated or rendered unfit to support this later development of the fungus. Thus, what is often referred to by observers without careful microscopic examination as "natural mortality" or "unexplained mortality" may be due to arrested stages of fungus attack without visible evidence, even with a hand lens. Other cases of "unexplained mortality" may be due to parasites which live internally and rarely if ever show on the exterior.

In the effectiveness of these entomogenous fungi under natural conditions there appear to be a number of contributing factors:

(*a*) In general, the fungi are favored by rainy, wet weather or high humidity, or by conditions on the plant and insects where moisture is sufficient for spore germination.

(*b*) Most entomogenous fungi appear to be favored by moderate

to warm temperatures, although the best temperatures for propagation vary greatly between species.

(*c*) Degree of light may be another factor; most fungi apparently are favored by shade, but others apparently depend on light for spore production, as the brown fungus, *Aegerita webberi* Faw. (20).

(*d*) Entomogenous fungi are dependent on favorable conditions for their distribution at the time when the insects begin to increase toward an injurious density. Some are spread by winds with or without driving rains, such as *Beauveria, Aspergillus, Metarrhizium* and *Verticillium,* while others are apparently dependent on contact with migrating insects of the same or different species, such as *Empusa fresenii* Now. and *Sorosporella uvella* (Krass.) Gd.

(*e*) Dense insect populations favor epidemics of some fungus species; a few, however, for example, *Aegerita webberi* Faw., the peculiar brown fungus on citrus, are only partly favored by density of the citrus whitefly larvae; this fungus has, in addition to internal hyphae, external mycelium that spreads over the surface of the leaf and may in suitable weather extend long distances on the leaf from one larva to another.

(*f*) Some organisms appear to be able to parasitize the insect more readily under one condition of nutrition of the host plant than under another condition (66, 67, 79).

It follows from these considerations that some of the entomogenous fungi are to be regarded, under certain conditions, as important factors in the biological control of insect pests, while others are apparently inefficient or of minor importance. Some of the same factors appear to govern their effectiveness, as those which influence the effectiveness of different entomophagous insects (63, 64, 76).

Artificial Use in Control. Whether the efficiency of parasitism can be increased by artifical means in any particular case depends, as it does in insect parasites, on some of the following considerations:

(*a*) If the conditions for natural distribution of a fungus are such that there is the maximum number of spores capable of infecting the maximum possible number of insects under prevailing environmental conditions, then no added results could be expected from artificial distribution without at the same time changing the conditions. A relationship of this kind may be known as the "satura-

tion point" for insect and fungus. This saturation point was probably the relationship of *Beauveria globulifera* (Speg.) Pic. to the chinch bug during the experiments where no increased mortality resulted from the distribution of additional spores (7). A saturation point might be expected most of the time from the abundance of wind-borne spores which such a fungus is capable of producing.

(*b*) When conditions are such that natural distribution is inefficient, *i.e.*, when this distribution is retarded or lags behind that necessary for maximum infection under prevailing conditions, then artificial distribution would be expected to increase the degree of infection. Whether artificial distribution would constitute an economical measure of control would depend, as it does with entomophagous insects, on what degree of increase could be effected by this means and its cost. It is believed that the natural distribution of a number of these fungi often lags far behind the possible maximum degree of infection, as in the aphis fungus of Florida, *Empusa fresenii* Now., which appears to depend for propagation on spores that are not readily distributed by wind and on the time of the insect's migration (23, 81). Artificial distribution preceding migration would appear to be suggested.

In certain situations in Florida, after a dry period or season the previous year, *Aschersonia* and *Aegerita* are not sufficiently abundant to efficiently infect whitefly larvae without artificial distribution at the beginning of the rainy periods in summer, usually June or July (87). If the "saturation point" has not been reached, then artificial distribution would increase mortality.

(*c*) As with insect parasites on insects, so with the fungus parasites, where the saturation point has been reached for natural infection under a given set of conditions, there is still some possibility of artificially manipulating or changing the natural conditions to shift the saturation point and to increase infection. Changes may be made in humidity by overhead irrigation to increase the moisture on the surface of leaves or fruits for a short time, or by other devices, as the growing of intercrops. This latter has been suggested in Florida in respect to the aphis fungus, *Empusa fresenii* Now. (81). With fungus diseases on plants it is known that such changes in conditions (rapid weather changes, *etc.*) do shift the saturation point and greatly increase infection (25).

(*d*) There is also the possible increase or decrease of suscepti-

bility of an insect to infection because of changed nutritional conditions influenced by the nutrition of the host plant. A case of this kind is mentioned later under the bacterium of the citrus red scale (66, 67).

One feature of this saturation point for infection is that it can not be certainly known that it is reached by finding the organism generally distributed in a given locality. This point may be reached at one particular time and not at another. Moreover, in many organisms, fungi or bacteria of common plant and animal diseases, it has been shown that the amount of infection may be greatly increased by the nature of the inoculum. Density and size of the inoculum of bacteria, or the "spore load" of fungi, is of great importance in breaking down resistance to infection (25).

While the use of these organisms in pest control has so far been limited, the future possibilities in their use, as of insect parasites on insects, depend, it would seem, on (*a*) devising efficient, economical methods of spread when there is an unsaturated condition of infection; (*b*) devising economical means of changing the environment on or about the plant to increase infection, *i.e.* to artificially shift the saturation point upward in order that the organisms present or being applied may have better conditions for infection; (*c*) changing the nutrition of the plants and concurrently that of the insects to make them more susceptible to infection by the parasitic organisms present or being applied.

FUNGUS PARASITES OF INSECTS

Chinch Bug Fungus. This fungus, *Beauveria globulifera* (Speg.) Pic. and formerly known as *Sporotrichum globuliferum,* is a conspicuous species forming a white growth over the dead bodies of insects. It has perhaps been referred to most often as a typical example of an entomogenous fungus, having been reported as occurring on at least 60 species of insects of various families in North America. Its parasitism, such as it is, is apparently not specialized, as is that of many entomogenous fungi. It is an example of fungi having wind-borne spores produced in great profusion, and is capable, therefore, of wide distribution in a short time, readily producing a saturation point for infection which is not so easily attained by certain other entomogenous fungi of more highly specialized parasitism. This probably accounts for the re-

ported failure to produce increased mortality by its artificial spread to the chinch bug, *Blissus leucopterus* (Say) (7). Petch, as the result of culture work on species of *Beauveria,* found numerous strains and concludes that "very many of the records of the host insects of the various species of *Beauveria* are open to question" (50). It would seem unsafe, therefore, to make generalizations from this example alone as to the value of entomogenous fungi.

Lefebvre, working with two species of *Beauveria* on the corn borer, found that *B. Bassiana* (Bals.) Vuill. was much more virulent than *B. globulifera* (Speg.) Pic. These two had been confused as one species by some authors. He concluded that the former had favorable potentialities for at least partial control of corn borer larvae, since they are exposed most of their lives to a relatively moist condition within succulent tissues (33).

Green Muscardine Fungus. Another conspicuous fungus with numerous, powdery, wind-borne spores is the green muscardine fungus, *Metarrhizium anisopliae* (Metsch.) Sor. This fungus, which is related to the penicilliums, has been identified on more than 60 species of insects, mostly beetles, in North America. It has been grown in pure cultures, and the spores in large quantities applied with a dusting machine in order to start epidemics earlier than would otherwise occur. Rorer in Trinidad found distribution of this fungus early in the season of value in increasing the mortality of the sugarcane froghopper, *Tomaspis varia* (F.) (61). For the May beetles, *Phyllophaga* spp., in Porto Rico, however, Stevenson concluded that its artificial distribution did not increase insect mortality sufficiently to make this practice of practical value (75).

Sorosporella of Cutworms. In contrast to the chinch bug fungus, the cutworm fungus, *Sorosporella uvella* (Krass.) Gd., a less known organism, completes its entire development in the body of its host, producing neither external growth nor wind-borne spores, and is an obligate parasite. As Speare (70) points out, while most mycologists are likely to overlook a fungus of this kind through a lack of familiarity with insects and their habits, entomologists, because of their lack of knowledge of mycology, usually give them at best scant attention. The mortality resulting from their attack is usually noted in such general terms as "mortality due to environmental conditions", "natural mortality" or "unexplained mortality". Certain yeast-like bodies known as blastocysts, produced within the blood

of the insect host, are carried in the circulation to all parts of the body, making the parasitism complete. Cutworms showing no external sign when dissected, are found to contain a brick-red powdery mass within the larval shell. This mass is made up of spherical reddish-colored resting spores. There is no doubt of the parasitism of the organism whenever the larvae become infected. Inoculation experiments on vigorous larvae show high infectivity of the spores which cause death in less than 10 days (70).

Fungi on Whiteflies of Citrus. Important examples of entomogenous fungi occur on species of whitefly larvae, *Dialeurodes* spp., in Florida. The following are most commonly found and a number of others occasionally: *Aschersonia aleyrodis* Webber, *A. goldiana* (S. & E.), *Aegerita webberi* Faw., *Fusarium aleyrodis* Petch, *Verticillium cinnamomeum* Petch. Some of these have been artificially distributed as means of biological control (1–6, 22, 87). It has been suspected that certain bacteria may also be parasitic on whitefly larvae, but no observation of their occurrence except in a minor way in connection with natural mortality (83) appears to have been reported.

When these organisms are present in certain moist situations in low hammocks of shaded situations in Florida and semitropical countries, the *Dialeurodes* species on citrus are practically controlled during some years. Morrill and Back (36), although concluding that in most orchards in Florida natural control can not be relied on, state: "There are, however, certain circumstances under which fungous parasites may be used to advantage. First may be mentioned the comparatively few citrus groves located in hammocks, with trees growing without regularity and with conditions such that fumigation or spraying with insecticides would be impracticable".

The difference of conclusions from experiments between Morrill and Back (36) who found no conclusive evidence that mortality of whitefly larvae could be markedly increased by artificial distribution by spraying with spores where the fungi were already present, and Berger (2, 4, 5) who found good evidence that it could be increased greatly by spraying spores at the proper season, may possibly be explained on the following assumption. The former probably experimented at a period of approximate saturation point for infection, while the latter probably experimented at periods

of unsaturation or of lag in possible infection for prevailing conditions. If this is true it would explain the differences in results.

Use of these fungi to increase natural control has been made principally in Florida (2, 87). The principle methods developed have consisted of simply spraying a suspension of the spores in water into trees infected with the insects. In some cases, fungus-bearing leaves were pinned to fungus-free leaves; in other cases, twigs containing fungus-bearing leaves were tied on branches of fungus-free trees (60). The brown fungus of the whitefly, *Aegerita webberi* Faw., soon after its discovery and before it had spread widely, was sometimes spread by placing young fungus-bearing trees so that their branches would intermingle with fungus-free branches of other trees (88). The source of material for spores to be sprayed was either leaves containing numerous well-developed pustules of the fungi or pure cultures containing numerous spores. The moist season of summer, according to Berger (4), was the most effective period for parasitizing the insects with spore suspensions.

One of the fungi, pure cultures of which are most used for biological control in Florida, is *Aschersonia aleyrodis* Webber. It appears as reddish pustules in and on the larvae. Webber followed with extensive observations the early spread of this fungus in certain orchards which had previously been severely injured by larvae of whiteflies (88). He refers to the striking recovery of trees coincident with the spread of this fungus after its first appearance in 1892. The population of larvae was so reduced in three years that no fruits had to be washed. Later, following the discovery that this fungus could readily be grown in pure cultures on sweet potato slices (18, 19), Berger developed a method of growing large quantities of this fungus and distributing it in pint and quart bottles for use in spraying trees with spore suspensions (2). *Aschersonia goldiana* Sacc. and Ellis is also being grown in the same way.

An important unusual type of entomogenous fungus also used for biological control of whitefly larvae in Florida is Webber's brown fungus, *Aegerita webberi* Faw. This species, in addition to a brown stroma that finally occupies the place of the larvae, has long colorless hyphae that extend over the entire under surfaces of leaves, killing every larva and then extending over the edges onto the upper surfaces and even along stems to the next leaves. Probably a light relationship causes the so-called sporodochia

consisting of inflated cells to form only on the upper surface. This cluster of inflated cells which contain appendages becomes detached and is carried by the wind, to function as spores (20).

The first spread of this fungus at Manatee, Florida, was described by Webber in 1897 (88). It was first found in March in a part of a five-acre orchard as a center with no trace in other orchards in the same sections. In nine months, or by December, it had spread with surprising rapidity so that it was difficult to find any living specimen of whitefly larva in the same five acres. By the following year the fungus had spread over a radius of about two miles, reducing the larvae coincident with its spread. Larvae of all stages were infected. Fawcett later proved experimentally the infectivity of the sporodochia, observing effects in nine days (20). The hyphae first appear in the interior of the larvae and the brown stroma burst through the edges in about 16 days. If weather is dry subsequent to infection, the dead larvae with interior hyphae may be desiccated and would then be classed by a casual observer as "unexplained mortality".

No method of successfully growing this fungus in pure cultures in large quantites has yet been developed, but its distribution has been effected in various ways, such as pinning leaves with pustules onto leaves containing live whitefly larvae, grinding up the pustules and stirring in water sprayed on the trees, or planting young fungus-bearing trees in such a way as to have the leaves intermingle. If leaves have the sporodochia abundantly developed on them, stirring leaves in water to get off the sporodochia and spraying the resultant suspension on whitefly-infected trees readily spreads the fungus. As to the effectiveness of this fungus under certain conditions, Morrill and Back (36) state: "The brown fungus has been so effective in controlling whitefly in certain low-lying hammock groves in Lee County [Florida] that it must be conceded this fungus has made artificial remedial measures unnecessary".

Fungi of Scale Insects. Scale insects under certain conditions of temperature, humidity and probably light and other factors may be attacked by a number of different fungi (39, 42. 60, 68). If conditions are unusually favorable in low-lying localities, as in Florida, most of the scale insects appear to remain at a low density level, doing little damage to the trees or fruit. During the dry season, however, in Florida generally during the winter and spring

months in higher, drier localities or regions exposed to wind, these insects become very abundant, unless control by natural enemies is supplemented by insecticides.

Evidence has been reported in Florida which shows that not all the increase of scale insects following bordeaux spraying is due, as previously thought (21, 24), to a killing of the fungi. It is found that road dust, lime and other materials not considered as fungicides also cause large increases there in purple scale insects and spider mites.[1] Several authors have concluded from spraying experiments in Florida that these increases can not be entirely attributed to prevention of fungous infection but to the effect of residues (37, 77, 78, 79). The diversity of opinion on this subject has been well stated (27): "Some believe that elimination of the fungi is the major factor; others, that the inert granular residue contained in the spray is the most important factor; and still others, that the increase is the result of the combination of the two factors" (27). The authors referred to present results in spraying trees infested with purple scale in Florida, which lead them to conclude that "the most important factor causing abnormal purple scale, *Lepidosaphes beckii* (Newm.), increase following use of fungicidal sprays is the inert granular residue content of the spray".

In connection with the interpretation of the results of these experiments with residue-producing sprays, certain conditions should be mentioned:

(*a*) The possible effect of the non-fungicidal and fungicidal materials on the tree itself in making conditions more favorable or less favorable for spread and infection of the fungi or for propagation of the insects (79).

(*b*) The possible effect of the material on the insect itself, its nutrition and development in making the insect more resistant or susceptible to infection by the fungi (58, 59).

(*c*) The possible effect of the material on the spread or infection of the fungus, even though the applied material may not kill the fungi already there.

(*d*) The possible effect of weather or other conditions immediately after application of the materials on the fungus and on the insects.

[1] Certain dusts containing lime also result in increases of California red mite, *Paratetranychus citri* McG., (26), but there appears to be no evidence that purple scale in California is increased by lime or by bordeaux.

It would appear that there is a complex of possible fluctuating factors that need to be unscrambled by experiments with controlled conditions for the insects, for the fungi themselves, and for the complex fungus-insect relationship, before it can be decided what part is played by the deposits or residues from applied materials, by nutrition of the tree and thereby nutrition of the insects, and by the parasitic organisms. Until such experimental work has been thoroughly carried out, the subject must largely remain in an observational and descriptive stage.

Many diverse entomogenous fungi are found on citrus scale insects (22, 42, 87). The most common are species of *Sphaerostilbe, Nectria, Podonectria, Myriangium, Hypocrella, Verticillium* and *Cephalosporium.* One of these, *Podonectria coccicola,* was one of the first entomogenous fungi noted in Florida. Hubbard in 1885 illustrated and described it as the "bark fungus" (28). Watson and Berger believe it to have probably been the main factor that reduced the destructiveness of the Glover scale, *Lepidosaphes gloverii* (Pack.), after this scale had been introduced into Florida at St. Augustine in the thirties of the last century (87). Trees at first were killed back each year by severe infestation, but after some years the scale was reduced by some unknown cause and the trees recovered. The reduction is now believed to have been caused, in part at least, by this fungus.

Well-controlled experimental work has been done on only a few of these scale-inhabiting fungi. Watson dipped branches of small citrus trees heavily infested with non-infected Florida red scale, *Chysomphalus aonidum* (L.) into spore suspensions of *Nectria diploa* (B. and C.) in April at Gainesville, Florida (86). By November every scale was killed. Viegas has reported experiments showing that *Cephalosporium lecanii* Zimm., when sprayed as spore suspensions, is an effective parasite in reducing green scale, *Coccus viridis* (Green), on coffee (82).

Fungi of Mealybugs. Species of *Aspergillus, Entomophthora* and *Empusa* are found as important entomogenous fungi on mealybugs. *Aspergillus parasiticus* Speare has been shown to be highly parasitic on sugar-cane mealybugs in Hawaii, and its effectiveness in killing young, freshly hatched larvae as readily as older ones has been experimentally demonstrated (69). It has been effective also in Puerto Rico (29). In California, pure cultures of an unnamed

species of *Aspergillus* produced 100% mortality in healthy mealybugs, *Pseudococcus gahani* Green and *Phenacoccus gossypii* (T. & Ckll.), at 21° C. in 72 hours and at 29° C. in 36 hours, while a large percentage of controls remained alive under the same conditions in a non-parasitic strain of *A. flavus* Link (8). This California mealybug fungus had given trouble in warm non-ventilated insectaries by attacking mealybugs being propagated on potato sprouts for rearing the entomphagous beetle, *Cryptolaemus montrouzieri* Muls., for liberation in citrus orchards (65).

Entomophthora fumosa Speare is considered by Speare as one of the chief factors, especially during periods of summer rains, in the natural control of the citrus mealybug, *Pseudococcus citri* (Risso), in Florida (71).

Fungi on Aphids. On aphids, species of *Empusa* and *Entomophthora* are highly parasitic and common. One of the well-known species is *Empusa muscae* Cohn, the cause of the so-called "frosted flies". Another species, *Entomophthora chromaphidis* Burger and Swain, was reported to parasitize about 88% of the walnut aphis, *Chromaphis juglandicola* Kltb., during one season (9).

The most important one on citrus is *Empusa fresenii* Now. This fungus is reported to be the chief factor in the control of the citrus aphid, *Aphis spiraecola* Patch, in Florida. Insects killed by the fungus are attached to the leaf solely by their proboscis, and appear as if standing on their heads. The abdomen and thorax become coated with tan-colored to light smoky brown, glistening spores. The interior body material is almost replaced by fungus. The spores are not wind-borne but depend for infection on migration of the insects which was found in Florida to be up to 500 yards (23, 30, 31, 80, 81). A colony of aphids is destroyed in a few days after the fungus attack.

Spicaria on Cottony Cushion Scale. Spicaria javanica Bally, forming loose white masses of mycelium covering the bodies of cottony cushion scale, *Icerya purchasi* Mask., is reported in Puerto Rico to have completely killed out this insect in certain orchards well protected by hills and bamboo windbreaks (90). The scales were not seen for at least seven years or during the time of observation, though in other places with less perfect windbreaks, the insect multiplied. The effectiveness of this fungus as a supplement to the entomophagous beetle, *Vedalia,* in Florida when the weather is warm and moist has also been reported (87).

Fungi on Mites. Mites are known to be parasitized by fungi. Charles (13) has described the fungus *Rhinotrichum depauperatum* found on the spider mite, *Paratetranychus yothersi* McG., on *Piaropus crassipes* (Mart.) Britton in Florida. This fungus consists of an effuse, cobwebby, white to pale gray mycelium in which the mites are enmeshed. The mites were killed experimentally in 18 hours when exposed to this fungus. The question arises as to whether the citrus rust mite fungus may be something of this nature.

An undetermined fungus has been reported on the citrus rust mite, *Phyllocoptes oleivorus* Ashm., in Florida. Speare and Yothers state that annually since 1912 rust mites had been observed to disappear as if by magic sometime after the beginning of the rainy season. This is usually the last of June or early in July. By the middle of September it was difficult to find a single mite present when they had been abundant before (72).

The sluggish mites had fungus filaments inside and the dead on the outside of their bodies.

BACTERIAL PARASITES OF INSECTS

A number of bacteria have been reported as causing definite diseases in insects of various kinds. The foul brood of bees due to *Bacillus larvae* White and a honeybee larval disease due to *Bacillus alvei* Chesshire & Cheyne are well-known examples. A disease of hornworm on tomato and tobacco, due to *Bacillus sphingidis* White, and septicemia of cutworms, due to *Proteus noctuarum* (White) Bergey, are other examples.

Recently a bacterium causing the milky disease in the Japanese beetle, *Popillia japonica* Newm., has been investigated and found to be effective in producing a high insect mortality (89). The causal organism is the spore-producing bacterium, *Bacillus popilliae* Dutky (16). Its relationship to the disease has been shown by inoculating several thousand healthy larvae. When healthy larvae come in contact with dead larvae left in the soil they contract the disease, which results in a high mortality. It has been found feasible to spread the disease artificially by means of spore dust derived from dead larvae, 1,500,000 larvae being used in producing over 25,000 pounds of spore dust. Diseased adults average about 500 million spores each, but larvae average about two billion spores each (32). It has recently been found that the adults, in actively migrating,

carry the organism while in the process of becoming diseased, so that it is suggested that adults be collected, inoculated, and liberated to spread the disease.

Another example is a rod-shaped bacterium causing a disease of epidemic proportions on the omnivorous looper, *Sabulodes caberata* Guenée, on avocados in San Diego County, California. Insects were readily killed by inoculations with pure cultures by spraying, rubbing or injecting the insects.[2]

Only two bacterial diseases of citrus insects have so far come to the author's attention, a disease of the mealybug, *Pseudococcus citri* (Risso), in Russia, and a disease of the California red scale, *Aonidiella aurantii* (Mask). The citrus mealybug was found to be infected by red bacterium, identified as a strain of *Bacterium prodigiosum,* which was isolated and shown experimentally to be virulent for several species of *Pseudococcus* (58).[3]

A spore-forming bacterium, designated as *Bacillus C,* has been found capable of killing the California red scale in California under certain conditions (66). If we except the mealybug bacterium, this is, so far as known, the first report of a scale insect infected with a disease-producing bacterium. Although *Bacillus* C was first isolated from soil in connection with denitrification studies and was grown on chitin, cellulose and other media (68), it has since been isolated many times from the bodies of red scale in the orchard.

Bacillus C is a large (6 by 1¼ μ) Gram-positive motile rod which forms spores in the equatorial position. Its motility is usually lost after a few days of growth on ordinary media. It grows singly, in twos end to end, and in chains of four or more.

Under laboratory conditions lemon fruits heavily infested with red scale immersed in a suspension of *Bacillus* C for two to four hours developed several days later a high mortality as compared to immersion into the same medium free from this bacterium.

In some seasons in past years, especially during or after moist weather, the California red scale has been noted to have had a very high mortality from some unknown cause. In one of those seasons, fungi were suspected to be one of the controlling factors (17). It is possible that this bacterium is responsible in part for epidemics of this kind when conditions are suitable for its abundant multiplication and spread to the insects. In preliminary field trials trees

[2] Unpublished work by Ira Ayres and D. F. Palmer.
[3] Referred to by Steinhaus (74, p. 133).

sprayed with suspensions of the bacteria or dusted with mixtures of spores and clay, the mortality of adult females was twice that of the corresponding checks (66). In time, the differences between the sprayed and unsprayed trees disappeared. A species of bacterium apparently identical with the one introduced was recovered in cultures from 90% of recently killed insects tested in this experiment.

Since death of the scale is accompanied by a significant decrease of soluble-nitrate content, it is postulated that the lethal effect of the bacillus is accompanied by nitrate reduction to nitrite inside the insect. This is further indicated by the fact that certain California red scales raised on sago palm or on detached lemons and grapefruit were found on analysis to have only a trace of nitrate and were resistant to the bacillus, while those raised under natural conditions had a greater nitrate content and proved to be susceptible. Moreover, when the scales were raised on sago palm which had been given abundant nitrate, the nitrate content of the scales increased and the latter became susceptible to the bacterium (67).

Previous observations on unusual California red scale mortality have been reported. Since the California red scale in 1934 was reduced by some natural means to a very small population (17), it is now suspected that *Bacillus* C may have been one of the main factors in this natural epidemic in the orchards. A heavy mortality also of the citricola scale, *Coccus pseudomagnoliarum* (Kuw.), was noted in California at the same time. Quayle states: "mortality occurred to an unprecedented extent in the more mature scales in the winter and early spring of 1934. Control work . . . was practically entirely omitted in 1934, 1935, and 1936. No such condition approaching this had occurred since the citricola scale became a pest of citrus more than 20 years previous" (59).

In a similar reduction of California red scale in Palestine in January, 1931, a high natural mortality was found, even where no control measures had been used. Young as well as older scales shriveled and turned a dirty violet color, and the scale for that season appeared to be well controlled by some natural means (10).

DISCUSSION AND SUMMARY

Entomogenous fungi range from species that possess a high degree of parasitism to those which are little more than saprophytes.

Their effectiveness is influenced by conditions of moisture, temperature, agencies of distribution, migration of the insects and apparently by nutrition, density or other conditions of the insect host.

The highly parasitic species appear to be important in bringing about certain degree of natural control which in favorable, special situations amounts to satisfactory commercial control. Others less parasitic are of only minor importance, while still others are of doubtful value and may be little more than saprophytes.

The chinch bug fungus, *Beauveria globulifera,* as an example of common widely distributed fungi, is reported on at least 60 species of insects and has abundant wind-borne spores. The failure to attain increased mortality by artificial distribution of this fungus has been often cited as an example of what may be expected from entomogenous fungi. It may be pointed out that this result might have been expected from a fungus of this kind which has many hosts and which produces such abundance of wind-borne spores that may become widespread and reach a "saturation point" under most all conditions suitable for infection. What was found with this fungus is not necessarily a criterion by which to judge possibilities in other fungi.

The green muscardine fungus, *Metarrhizium anisopliae,* with similar characteristics as to wind-borne spores, has been used commercially for an early start of epidemics of froghoppers in Trinidad but failed to be of practical value on May beetles in Puerto Rico. There was probably a sufficient lag in spore saturation when used in the first case and more nearly saturation in the second.

In contrast, *Sorosporella* of cutworms produces neither external growth nor wind-borne spores and completes its development within the insect body, producing complete parasitism in 10 days by means of yeast-like bodies within the blood.

Among a number of fungi that parasitize the *Dialeurodes* or whitefly larvae, *Aschersonia aleyrodis* and *Aegerita webberi* are outstanding examples. Under conditions like those in parts of Florida these are spread artificially to increase their efficiency at certain seasons of non-saturation. Under certain conditions, these fungi without artificial aid appear to keep the insects at a low level and in some conditions to aid in producing commercial control. Differences in conclusions as to their value for artificial use may be due to trials under different degrees of spore saturation.

Among the fungi parasitic on scale insects, some of the most important are species of *Sphaerostilbe, Nectria, Podonectria* and *Myriangium*. In conditions of moist low-lying localities in Florida most scale insects in association with these fungi remain at a low level. It has been pointed out, however, from certain recent observations, that the efficiency of entomogenous fungi on purple scale can not be entirely judged by the phenomenal increase of this scale by spraying with bordeaux mixture or other residue-depositing fungicides. Non-fungicide residue-depositing mixtures also cause increases in purple scale. Other factors making it more favorable for their development appear to account for a considerable portion of this increase.

Species of *Aspergillus* and *Entomophthora* are discussed as important parasites on mealybugs, *Empusa* and *Entomophthora* on aphids, a species of *Spicaria* on cottony cushion scale, and one of *Rhinotrichum* and an undetermined fungus on mites.

Attention has recently been directed to bacterial parasites of insects through the success in the work with the milky disease of the Japanese beetle.

A spore-forming bacterium, known as *Bacillus* C, has recently been found capable under certain conditions of killing the California red scale. The susceptibility to attack appears to be increased greatly by the increase of nitrates in the substrate on which the insect feeds.

There appears to have been in the past a tendency to judge the possibilities in this line of investigation by the failure of some of the past experiments to show outstanding control. What is needed is to determine more definitely not only the rôle which these entomogenous fungi and bacteria play in natural control, but also to explore further the possibilities of increasing their efficiency by artificial spread in situations where the saturation point is not reached under natural conditions.

Much attention is being given to the discovery, introduction and artificial spreading of entomophagous insects and to finding ways of increasing their efficiency. The comparatively few that have given outstanding control have justified this large effort. Greater attention is needed in exploring the possibilities from similar work with various insect-destroying fungi and bacteria, and possibly insect-destroying viruses. More cooperative research by plant

pathologists and entomologists should yield important results in this largely unexplored field.

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RECENT STUDIES ON INHERITANCE OF QUANTITATIVE CHARACTERS IN PLANTS

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INTRODUCTION

Quantitative characters, by definition, relate to measurable differences in degree rather than in kind, and in their inheritance usually exhibit a continuous range of variability in segregating populations. This group of hereditary characteristics is particularly susceptible to environmental influences, and it should be emphasized that it is the manner of reaction under particular conditions that is inherited and not the character itself (68, 212). As pointed out by Dobzhansky and Holz (46): "Genes produce not characters but physiological states which, through interactions with the physiological states induced by all other genes of the organism and with the environmental influences, cause the development to assume a definite course and the individual to display certain characters at a given stage of the developmental process".

An obvious distinction can be made between typical "quantitative" characters and those typically relating to "qualitative" variation, in which unlike discontinuous classes of segregants can be observed; yet it is equally evident that there is no sharp line of demarcation between the two groups, and the terms should be used merely as convenient descriptive expressions rather than as inflexible categories of classification. Mather (112, 220) has suggested that the numerous genes determining quantitative variation, which have individual effects that are small compared to the total nonheritable fluctuations (minor, buffer or polygenes), differ from those determining qualitative variation (major, switch or oligogenes) by acting at a later stage in ontogenetic development. We would prefer, however, to suspend judgment as to differences in the nature and mode of action between these two types of genes until further evidence is available (see 191).

An effort has been made in preparing this paper to review the pertinent botanical literature, mostly during the past six years

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(1937–'43), on inheritance of quantitative characters. Publications in related fields have been referred to where it was considered that they provided clues to further elucidation of this problem.

THE GENETICS OF QUANTITATIVE CHARACTER INHERITANCE

Gene Number, "Genetic Coefficients" and Restrictions on Character Recombination

The most important conception in a genetic interpretation of the continuous variability observed in families segregating for hereditary differences in quantity has been the multiple factor hypothesis (polymerism in European literature), promulgated by Nilsson-Ehle and by East. According to this interpretation, inheritance of typical quantitative characters is under the control of a number of genes or factors which are similar and relatively small in effect, usually incompletely dominant in expression and which act in a cumulative manner. Most published experimental data are in agreement with the general statistical requirements of this hypothesis, and the literature on the subject is voluminous owing primarily to the fact that the majority of species differences and characters of practical value in agriculture are under multiple genic control. Brief reviews of work on quantitative inheritance in crop plants are included in the recent text of Hayes and Immer (68) and original papers on genetic studies with cucumber (74). Medicago (12) and barley (26) will serve as recent examples to illustrate the type of data, obtained with agricultural material, that is generally considered amenable to a multiple factor interpretation.

From the time of the early workers on size inheritance numerous attempts have been made to estimate the number of genes involved in a particular quantitative difference. The method used most often has been to calculate the frequency of recovery of parental classes; a high frequency was taken to indicate few genes and a low one or failure to recover the parental extremes was taken to indicate that many genes were responsible for the difference between the original types. For the most part the methods used and the conclusions reached provided little more than crude approximations of gene number, as the authors were fully aware.

"Student" (185) concluded from calculations on data involving selection experiments for oil content in maize that, for the character under consideration, there was some evidence for a gene number

"at least of the order of 20–40, possibly of 200–400, and not at all likely to be of the order 5–10". Rasmusson (149) stated that the Swedish group of geneticists and plant breeders "seem to be unanimous in assuming 100–200 genes for most quantitative characters in crosses between types not too closely related". The formulae of Wright (210) for estimating the minimum number of genes and the number with manifold effects have been used by Charles and Goodwin (35) to analyze hereditary differences between the leaf characters of two species of goldenrod. They calculated that a minimum of 21 genes determined the differences between the leaf characters and that about twice as many were probably operating to control all the morphologically distinguishable characteristics between the two species.

The writer has estimated (179), by use of a formula of Wright, that not less than 12 genes are involved in determining the difference in corolla size between two species of *Nicotiana*. The prerequisite assumptions to all such estimations, however, are difficult to prove. In the *Nicotiana* cross, for example, it is apparently incorrect to assume that all the genes for small size are concentrated in the small-flowered parent, since certain extra chromosomes of this species cause enlargement of corolla parts (181).

Anderson (9) has pointed out that if the number of genes involved in quantitative character differences is as large as ordinarily postulated, then "all the multiple factor characters of an organism will be tightly linked with each other, without regard to the further restrictions imposed by frequencies of recombinations". Linkage obviously seriously restricts recombinations in the F_2, and in a particular *Nicotiana* cross, where gametic elimination, zygotic elimination and pleiotropism (defined below) also play a part, Anderson has calculated that the actual F_2 recombinations constitute less than 1/64 of the total imaginable. The writer has worked with the *Nicotiana* species and hybrids under consideration above and can add that there are also developmental restrictions to pattern recombination which, by themselves, limit the number of possible recombinations to only about two-thirds of those "imaginable". It can be shown that the genes determine relationships during development rather than absolute dimensions, so that recombinations of the length of one species with the width of another, for example, cannot be realized because of the limiting conditions imposed by relative growth.

Problems concerned with gene number, manifold or pleiotropic effects, "genetic coefficients" (defined below), developmental patterns and restrictions on character recombination are closely tied up with each other and all are intimately involved in the genetic interpretation of quantitative character inheritance. One of the long-recognized difficulties in analyzing size traits has been that many genes influence one character. The situation may be further complicated by the fact that a single gene can influence several characters by initiating one or more primary effects. This latter phenomenon is known as "pleiotropism" in the broadest sense of the term. It has been suggested by Anderson and Owenby (11) that interspecific variation is not a matter of random character differences but rather one of "harmoniously integrated tendencies" based on fundamental differentiating qualities, known as "genetic coefficients", which may produce basically similar differences throughout the organs of a plant. For example, the larger leaves, thicker stem and coarser texture of one species compared to another might be attributable to a generally larger cell size, the genetic coefficient. It was recommended (11) that species hybrids be studied in terms of genetic coefficients rather than by analyses of such complex characters as plant height or leaf length in order to obtain more direct evidence as to differences between the related germplasms. Most genetic coefficients would probably be found to be under multiple genic control.

It has been indicated by Whaley (178, 200, 201, 202) that the size of determinate plant organs (flower, fruit and leaf) is dependent upon the size of the meristem from which they are produced, at least in plants with relatively indeterminate growth, as in the tomato. This observation implies that a form with larger flowers than another would also have larger fruits and probably larger leaves if the relationship is not too disturbed by the environment. While such an association may be the rule in *Lycopersicum, Cucurbita* and *Lagenaria,* it obviously does not hold for all types of plants. We have measured two closely related strains of *Nicotiana rustica,* for example, and have found that the average leaf length of strain A was 10.7 ± 0.98 inches and of strain B 13.2 ± 1.08 inches, while the average corolla length of A was 16.6 ± 1.45 mm. and of B 14.9 ± 0.83 mm. Whaley's suggestion and the more general one of genetic coefficients are undoubtedly significant, but it should be

borne in mind that a given set of genes does not necessarily produce a similar recognizable external morphological effect in all plant parts, even though a basic property, such as cell size, is affected similarly throughout the organism.

The concept of multiple alleles at one locus, or possibly closely linked loci, rather than multiple genes at relatively independent loci has been useful in explaining certain hereditary phenomena of a quantitative nature. Hutchinson, Silow and others (75, 77, 166) were able to interpret differences in leaf shape in Asiatic cottons on the basis of at least five alleles at the L locus which affected sinus depth and lobe width. Hammond (62) has shown that the genes for leaf shape act by controlling correlations between growth rates in various dimensions. A system of multiple alleles has also been used to explain the results of genetic studies on bristle hairlines in *Galeopsis pubescens* (128), flower form in *Salpiglossis* (41), glume shape in *Triticum* (192) and petal flecking in *Godetia* (69).

The principle of multiple genic control is generally accepted in genetic explanations of quantitative inheritance, yet some characteristics involving hereditary differences in quantity are apparently determined by relatively few genes, and others, as plant height in maize, may be either multiple or monogenic in their inheritance. In view of these considerations and our ignorance concerning the basic difference, if any, between the genes controlling qualitative and quantitative characters, it was thought advisable, in a comprehensive review of the subject, to cite some recently published examples of hereditary traits involving size and shape which were found to be under simple genic control.

The characters dwarf habit (64, 74, 76, 87, 94), double flowers (25, 199) and differences in leaf shape (64, 147, 157) were reported in various species to be dependent on the action of single recessive genes. Other characters, such as fruit shape in *Capsicum* (121) and peach (95) and double flowers in the carnation (80), were found to be regulated in their inheritance by a single gene difference that was dominant to normal.

Lack of dominance, so characteristic of polygenic action, is less commonly observed in character differences subject to monogenic control, but has been reported, *e.g.*, for the dwarf-red type (115) and for okra-leaf shape (157) in Upland cotton. In a species with a low chromosome number and presumably relatively fewer genes,

some quantitative characters might be expected to be relatively simple in their inheritance. This seems to be the case in barley which has only seven pairs of chromosomes, for in the first linkage group there are at least eight characters involving differences in quantity that give monogenic ratios (162).

It is probable that for the most part where simple Mendelian ratios occur the aberrant types represent a physiologically restricted condition. East (48, 49) has suggested that species have evolved by a progressive accumulation of small, abundant, constructive mutations with quantitative effects and that the more obvious "defective" mutations that are more frequently studied in genetics are relatively unimportant in evolution. The concept of physiologically defective genes should not be confused with that of typical quantitative factors whose action is to reduce size, for small size may be advantageous (96) and there is evidence that reductive genes play an active rôle in typical size inheritance phenomena (181).

Gene Action, Dominance, Heterosis and Skewness

Much of the recent discussion on the genetics of quantitative character inheritance has been concerned with the nature of gene action, dominance relations of alleles and interactions between genes. The conclusions that have been drawn are, for the most part, tentative, since adequate experiments that would furnish definite answers to these problems are difficult to devise and have not yet been performed. Statistics expressing averages, standard deviations and skewness have provided the main material from which genetic inductions have been made. In the footnote[2] below

[2] *Interaction*—gene action of such a nature that a certain gene substitution acts differently in combination with one genotypic background than with another. This definition is intentionally limited in scope and is essentially statistical when applied to quantitative data. The term is used frequently in genetics in the more general sense that the expression of certain (or all) characters is the end product of the combined action, *i.e.*, interaction, of several or all of the genes of the genotype; however, as a rule, it is in the more restricted meaning, as defined above, that the word "interaction" has been used in publications on quantitative inheritance.

Arithmetic action—each gene substitution adds or subtracts its contribution to that of the residual genotype. If the absolute amount added to the phenotype is the same regardless of the other genes present the gene in question would be considered as having independent arithmetic action.

Additive action—arithmetically accumulative and usually implying lack of interaction.

Geometric action—each gene substitution multiplies or divides the residual genotypic value by a certain amount. The absolute phenotypic contribution of the gene would vary according to the magnitude of the residual genotype,

we have listed, as an aid to the discussion to follow, brief explanations of some of the terms encountered frequently in papers on quantitative inheritance.

The results obtained from crosses between types differing in quantitative characters have been extremely varied, owing undoubtedly to complex anatomical and physiological conditions as well as to those of a genetic nature. Some workers have attempted to examine their data for evidence indicating whether the gene action is more nearly arithmetic or geometric in effect, though neither scheme is expected to apply strictly for all genes or for all organisms. "It seems likely, on the whole, that the genes determining any particular size difference would be found, if isolated singly, to be rather diverse in nature of action and in synergetic relations as well as in magnitude of effect and degree of dominance. But the isolation of monogenic differences is generally so difficult in the case of quantitative characters that it is often practicable only to determine which of commonly proposed simple schemes of inheritance comes nearest to compatibility with the data" (36).

One type of result obtained frequently in studies on size inheritance is characterized by the F_1 mean approaching the geometric mean between the parents and a positively skewed frequency distribution for F_2 measurements. These data have been interpreted by some to indicate a probable geometric gene action (34, 36, 103, 104, 142, 143, 144, 145, 170, 179, 181); others have suggested (96) that they could be explained mainly on the basis of arithmetic effects with partial dominance of genes for small size, and it is also possible that the metrical bias observed has no genetical significance (111).

The arguments advanced by Lindstrom (96) for favoring the arithmetic scheme with partial dominance of genes for small size were based mainly on evidence for a decrease in the mean variability and positive skewness in a $4n$ F_2 compared to a corresponding $2n$ for measurements on fruit size in tomato. It can be shown,

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but if it acts as a fixed multiplier the gene would be considered independent and geometric in action.

Positive skewness—a type of departure from a normal frequency distribution curve characterized by the median being to the left of the mean and a "long tail" to the right. A skewed distribution in the opposite direction is called negative.

Metrical bias—skewness in a + or − direction caused by an "inherent" relation between the scale of measurement and phenotypic expression. It may or may not have genetical significance and can be removed by an appropriate transformation of scale (53, 111).

however, that these same results would be expected if the genes acted in a geometric manner without dominance or interaction, and, furthermore, if many genes determine fruit size (as seems to be generally agreed is the case) one would not expect to find pronounced skewness due to dominance in a relatively small sample population.

We are inclined to favor a general geometric interpretation, at least for the results with fruit size in tomatoes and squash and corolla size in *Nicotiana,* because it has a reasonable morphological and physiological basis (104, 171) and because the empirical statistics are in remarkably close agreement with theoretical expectation (36, 103, 181). The suggestion that hereditary factors controlling size, growth or quantity may have geometric, multiplicative, percentage or exponential effects is not a new idea; it can be found in earlier publications, notably those of Galton (1879), East (1913), Groth (1914), Zeleny (1920) and Wright (1922). Evidence from morphology indicates (71, 104, 173) that gene substitutions act by controlling such properties as cell size, number of cell divisions or the integrated growth process and, therefore, might be expected to have a general multiplicative effect on the size of a mature organ or organism. However, any measured quantitative character is, in itself, a complex biological entity subject during development to a variety of stresses, and a gene substitution affecting a particular histological condition should not necessarily be expected to produce a strictly geometric effect on the end product. The results of experiments on quantitative inheritance in *Zea mays,* for example, are in general more amenable to an arithmetic interpretation; and, from the great variety of data with other plants and animals, it appears unlikely that a simple consistent type of gene action can apply to all.

Data on corolla size in a series of interspecific polyploid hybrids of *Nicotiana* (181) afforded an illustration of both a simple and a complex relationship in size inheritance phenomena. It was found that each genome substitution had an apparently simple geometric effect on corolla size and that polyploidy acted as a multiplier only on the size of the tubular part of the corolla and not on the length of the limb. The polyploidy effect is essentially a histological problem but it does indicate that if a gene substitution affected only cell size it would not necessarily produce strictly geometric effects on a particular quantitative character. On the other hand, typical "size

genes" probably act in a more harmonious manner, controlling coordinated growth processes rather than one property. In the above experiments a modified multiplicative scheme, in which the numerical value of each locus was considered to be equal to the geometric mean of the alleles involved, was adopted as a consistent, workable system for explaining the genetic results in both diploids and polyploids. It is probable that the multiplying values of most of the genes producing increases in size are around 1.1 or 1.2 and those causing decreases are around 0.8 or 0.9.

From the extensive data on first generation hybrids between types that differ in quantitative characters it is evident that the F_1 mean may exceed the value of the larger parent; be less than that of the smaller (168); or have almost any intermediate value. The latter result is most commonly observed in studies on size inheritance and has led to the belief that, in general, most genes controlling quantitative inheritance are incompletely dominant in phenotypic expression.

Hybrid vigor or plus heterosis, in which the F_1 is larger than either parent or at least exceeds the mean between the two parents, is also a frequently observed phenomenon and, in the currently most accepted genetic interpretation first proposed by Jones, is explained on the basis of an accumulation (in the heterozygous condition) of dominant genes favorable for growth. Dominance is assumed whether heterosis is considered "normal" vigor achieved through heterozygosity by the hiding of deleterious recessives, as suggested by Collins, or "supernormal" growth caused by an "excessive" accumulation of advantageous genes. The convergent improvement method for corn breeding outlined by Richey is based upon and affords a means for testing this dominance hypothesis; and the results of recent experiments (68, 221) tend to confirm the theory that at least part of the heterotic effect can be explained on this basis. It is reasonable to consider heterosis as one type of result in the general category of quantitative inheritance, and it appears likely, therefore, that the genes affecting quantitative characters, like those producing qualitative effects, may manifest different degrees of dominance.

East (50) proposed another genetic explanation for heterosis in which the increased vigor was attributed in large measure to the accumulative action of multiple alleles. He assumed that the genes

concerned with heterosis lack dominance in the classical sense and control "non-defective" physiological reactions. Mutations, that occur frequently at the loci involved, produce alleles with slightly different physiological action. When certain of the divergent alleles are combined in the heterozygous condition they act in a complementary manner, thus producing a more efficient physiological condition which finds phenotypical expression as hybrid vigor.

R. A. Fisher and certain British geneticists (53, 78, 111) have maintained that heterosis is due to a progressive selection for dominant + genes having taken place and that in unselected material dominant genes that act on growth in a + and in a – direction would be present in a genotype in approximately equal numbers. In regard to the phenomenon of dominance the conclusions of Silow (166), based on observations pertaining to the genetic analysis of leaf shape in cotton, are of interest. He is of the opinion that dominance is best regarded as a function of allele interaction, dependent upon the magnitude of the gene's effect relative to the possible range in expression of the character affected, as well as upon other genes working toward the same result. The system may be conceived as an interplay of "threshold" and "saturation" effects.

A recent comprehensive review of the subject of heterosis has been prepared by Whaley (203) who has discussed the various explanatory hypotheses. In conclusion, the solution of the problem of heterosis, like that of the more general one of quantitative inheritance, awaits the presentation of more conclusive experimental evidence in support of any one of the explanations offered.

Mather (108, 110, 111, 112, 113) and Wigan (205, 206) have published papers recently on the rôle of quantitative inheritance in relation to selection and evolution. The general concepts presented have been summarized in a review article by Mather (111) and may be outlined in brief as follows: The greater part of species differentiation is quantitative or polygenic, *i.e.*, controlled by many genes with similar action whose individual effects are small compared to the total non-heritable fluctuation, and variability is maintained at a high level as an essential for prospective adaptive and evolutionary change. By the action of natural selection, so-called "balanced" combinations of polygenes are built up within each chromosome. Systems so produced will be characterized by "close adaption to the optimum, great variability storage and slow variabil-

ity release" (111), and may be pictured genetically as composed of dominant genes acting to increase the expression of a character distributed throughout the chromosome and combined (preferably by close linkage in the repulsion phase) with an approximately equal number of genes acting to decrease the expression of the character. Variability is released by segregation and recombination. Balance is disturbed in recombinations, and the resulting phenotypic variability is acted upon by selection. The response to selection and random elimination of alleles reduced variability which, however, is replenished by mutation.

The shape of the frequency distribution curve has been used by some as a basis for interpreting their results on quantitative inheritance. Caution should be exercised, however, in interpreting skewness, for different causes, equally likely *a priori* and difficult to distinguish, may produce skewness in either direction; furthermore, a normal distribution may indicate balance between opposing tendencies rather than freedom from them.

Positive skewness may be caused by a predominance of dominant genes for decreasing size, an approach to a physiological lower limit of phenotypic expression, interactions of such a nature that each gene acting to reduce size has progressively less effect the more there are acting in the same direction, or by geometric action of the genes. Negative skewness may be caused by a preponderance of dominant genes for increasing size, an approach to a physiological upper limit of phenotypic expression, or by interactions of such a nature that each gene acting to increase size has progressively less effect the more there are acting in the same direction (149).

Genes obviously interact, in a general sense, to produce characters, and some with major effects (see 167) are known to interact in the more specific sense defined in the footnote on page 354; yet there is no clear evidence that this latter type of interaction occurs between typical multiple genes controlling the inheritance of quantitative characters. Mather (111) has pointed out that the interactions reported in *Pisum* (150) and *Lycopersicum* (40) could be due to metrical bias; nevertheless, he is of the opinion, and most investigators would no doubt agree, that until more information is available it would be discreet to suppose that any type of interaction shown by genes with major effects may also be found among the so-called polygenes. Powers (141) concluded that there was no

general rule for interaction between genes determining quantitative characters, but he observed that genes favorable to high weight of seed per plant in *Hordeum* gave greater increases over their alleles in combination with non-allelic genes for higher yield than with those for lower yield.

The concepts of directional interaction, causing skewness in one direction, and of physiological limits should be distinguished in theory, for the former is genetic and could be independent of the magnitude of the phenotype, while the latter is physiological, directly dependent on it, and would be found only where certain bounds were exceeded. Skewness due to physiological limits might occur in a homozygous line and in this way would be distinguishable from that due to dominant genes which necessarily would be the result of segregation in heterozygotes (149). Skewness would be accentuated if a character were determined by relatively few dominant genes or if some of the genes had major effects.

If a wide enough range of phenotypic values were available, physiological limits might conceivably be approached in both directions. We apparently have an example of this in some unpublished data collected in the Division of Tobacco Investigations on selection for low and for high nicotine content in *Nicotiana tabacum*. Frequency curves for alkaloid content in presumably homozygous low nicotine selections that had on an average around 0.5% of the alkaloid in dried leaves, were positively skewed, while the distributions in high nicotine selections (4.5–5.0%) were negatively skewed. A sensible interpretation of the results with the selections for high nicotine would be that there is a physiological upper limit to the amount of nicotine that can be accumulated within the tobacco leaf which, in the strains under consideration, is around 4.5 to 5.0 per cent. The positive skewness in low nicotine selections may be attributable to an inherent essentiality of nicotine, however low in concentration, to life processes in the tobacco plant.

Another example of data exhibiting + skewness at the lower end of a scale and – skewness at the upper is found in the distribution curves for "total index values" in comparisons between species in the genera *Tradescantia* (5), *Solidago* (58), *Iris* (153) and *Aster* (196). The indices were only arbitrary quantitative measures derived by crudely combining a group of observed characters by which the species are differentiated, but the consistent shape of the

distribution curves may indicate that the combined characteristics accumulated within a natural species do, in some way, approach morphological or physiological limits of development along a particular evolutionary line.

The skewness of metrical bias may be in either direction, depending upon the relation of the scale of measurement "to the unknown 'scale', on which the organisms' physiological processes work" (111), as log. to antilog.; but its effect would be consistently in one direction for the data on a particular quantitative character. Negative skewness in frequency distributions for measurements on plant height in barley was interpreted as due mainly or wholly to metrical bias attributable to environmental influence (53).

Other conditions that may affect skewness in either direction are interactions that are not unidirectional (*e.g.*, different conditions of epistasis and complementary gene action), the amount and type of linkage, and differences in the proportional contribution of the common residual genotype to that of segregating genes in making up the total value of the phenotype.

Methods of Analysis

The nature of quantitative character inheritance makes it necessary to record experimental results in some form of measurement and, for final analysis, to treat the data biometrically. In addition to the use of generally accepted methods of experimental design (52) and statistical analysis (51), formulae that refer more specifically to quantitative inheritance have been developed and used. A few that might be mentioned here are the use of third degree statistics in analyzing skewness (53), methods for separating environmental from genetic variation (209, 36, 140, 145), estimation of the number of gene substitutions determining an hereditary difference (210, 35), a "mathematical notation . . . for expressing the . . . morphological hiatus between two species" (11), criteria for distinguishing between the results of geometric *vs.* arithmetic gene action (36), and a method for determining the degree of influence of size factors with general and with local effects (208).

Other analytical methods, more cytogenetic than mathematical, have been developed for the purpose of investigating quantitative inheritance by breaking down the usual continuous segregation into a discontinuous one. This can be accomplished by utilizing inver-

In other species, such as *Cucurbita Pepo* (169), there was little difference in the relative growth constant in types with different growth shapes; but differences were established in the primordia very early in development and were maintained to maturity. Similarly, in Houghtaling's (71) investigations on tomato fruits, it was shown that shape differences were established in the ovary primordium before flowering as a result of differential growth rates between polar and equatorial dimensions; and subsequent relative growth rates were the same for all forms (see also 104 and 213).

These developmental relationships may be expressed mathematically by using Huxley's formula for relative (heterogonic or allometric) growth, namely, $y = bx^k$. In analyzing shape differences x and y have been taken as two dimensions of an organ; k is the constant ratio between their growth rates (the slope of the line); and b is a constant representing an initial relation between the dimensions.

A study of relative growth rates has been found useful in recent investigations on the inheritance of leaf shape in golden-rod (59), *Aster* (43), *Nasturtium* (204), cotton and other genera (62); and on the shape of the ovary wall in *Iris* (154). Commonly there is a sudden break in the direction of the relative growth curve which in *Solidago* (59) was found to be correlated with cessation of cell division and initiation of rapid cell enlargement.

Histological Conditions Associated with the Development of Size and Shape

Research on correlations between differences in size and shape of organs during development and their constituent cells is a field of investigation that has only recently begun to be explored. Reviewing the evidence from studies on fruit size in the Cucurbitaceae regarding relations between the size of cell and organ, Sinnott (173) concluded that "it is the organ or body which shows the more simple and unitary growth program in the attainment of a specific size, and the cells of which the organ is composed display a much greater diversity in size, number and rate of change". This conclusion was based on four groups of evidence that may be outlined as follows:

a) The fruit develops according to a regular growth cycle that is very similar in all types despite differences in relations between fruit size and the size and number of the cells. The general histo-

logical features of fruit development in cucurbits are that tissue growth takes place at first chiefly by cell multiplication accompanied by a slow increase in cell size; and, after a specific cell size is reached, division ceases and all further growth of this tissue is by cell expansion. This is also essentially the situation in the development of tomato fruits (71, 104) and the leaf of goldenrod (59).

b) Growth of the fruit proceeds at a constant logarithmic rate, even when there is an abrupt shift from cell multiplication to increase by cell expansion.

c) Growth of the plant proceeds at a constant logarithmic rate though the volume of the meristematic cells decreases (200, 201).

d) From measurements on growth in root tips it has been shown that after division ceases in a given lineage, elongation of each cell is at first more rapid at its basal (proximal) end and later at its apical one. "It is thus brought about not by a uniform expansion of one cell after another in a series toward the apex, but rather by a "wave" of elongation which proceeds apically and affects first one end of each cell and then the other. This is not what one would expect to happen if growth of the organ were the result of growth of relatively independent cellular units" (173).

Bindloss (28) found no positive relation between meristematic cell length and mature stem length in a developmental study of tall and dwarf races of tomato; but the former had a longer meristematic region, thus accounting for greater height by making a greater number of cell generations possible. The length of panicles in larger forms of rice compared to dwarf types was ascribed to more active cell divisions (133). No difference in cell size was noted. Abbe and Phinney (1) reported that dwarf maize plants (d_1d_1 in constitution) were shorter than normals, owing to the fact that cell division and enlargement had proceeded more slowly.

It is evident that differences in cell size or number or both may be found in plants that differ in organ size.

Developmental anatomical studies have been fruitful in yielding information on the morphological basis for hereditary differences in shape. It has been shown in the cucurbits that the determinative basis of form is independent of organ size and thus, according to Sinnott (173), of the number and size of the cells that compose the organ. There was no essential difference in the shape of component cells of races with different shaped fruits. It would appear,

therefore, that the relation between the number of cell divisions in one plane compared to those in another would be the controlling factor in determining shape differences.

In confirmation of this hypothesis, Sinnott (173) found from developmental studies that in cucurbit fruits where length and width increase at an equal rate mitoses are equally abundant at all angles, whereas in the club gourd where length grows more rapidly than width there is an excess of figures which make a relatively small angle with the axis. The genotype of the organism appears to have a directive influence by causing a coordinated swinging of the angle of the mitotic figure, cell plate and new cell wall into the required position (173).

Hammond (62) found that in cotton "Shape differences between broad and narrow leaves are essentially due to differences in relative numbers of cells in the length and width planes". The relatively longer and narrower leaf of *Solidago sempervirens* compared to *S. rugosa* was reported (59) to be "due to less pronounced marginal cell division, to greater elongation of the cells parallel to the midrib, and to prolonged, polarized cell division in the basal, petiolar portion". It was shown that differences in leaf shape between two species of *Aster* were attributable partly to limitations on the number and direction of cell divisions and the extent of cell enlargement (43).

Leaf pattern in a cross between two species of *Tropaeolum* (204) was found to be determined very early in development by differential cell division in such a way that in regions where multiplication was more rapid, small cells with greater expansion potencies were laid down. Final shape was determined by the extent to which cell enlargement developed the potential pattern of the juvenile leaf, and was controlled mainly by two genes with cumulative effects.

Differences in the relative growth rate of certain regions of *Iris* ovaries were reported to be dependent chiefly on differences in the relative rate of cell division (155, 156).

The effect of polyploidy on size and shape should be mentioned here, though no attempt to review the literature on this subject will be made. Generally, an increase in chromosome number causes an increase in cell size which frequently results in larger plants and organs, provided an upper limit of tolerance is not surpassed. The main effect of polyploidy on shape is to bring about proportionately

greater increases in width than in length so that the organs are relatively wider and thicker in the types with higher numbers of chromosomes (175, 180, 181, 215).

Experimental Evidence Indicating Possible Physiological Bases for Quantitative Inheritance

It is generally recognized that the visible expression of gene action is the manifestation of fundamental physiological processes which, in turn, rest ultimately on a physico-chemical basis. Though we know little of the complex series of chemical and physical changes involved in the development of quantitative traits, a few experiments have been reported recently which deal with the physiological basis of hereditary growth differences. These investigations were concerned chiefly with inherited differences in the production of growth-regulatory substances and with hereditary variation in plant nutrition. Any statements relating these experimental results to the physiological basis for quantitative inheritance should be qualified, however, for it is possible that no such correlation exists, though the speculation is attractive.

A number of genetic dwarf types in maize were found by Overbeek (136) to produce auxin at a lower rate than their normal sibs, and tissues of the recessive known as "nana dwarf" inactivated auxin more rapidly than tissues of normal plants. Goodwin (57, 59) observed, from a study of the amount of auxin diffused from the leaf bases of two species of goldenrod, that more was obtainable from *Solidago sempervirens* than from *S. rugosa*. He inferred that certain genetic differences in leaf size, leaf shape and type of inflorescence could be attributed to differences in the amount of auxin in each species. Two species of *Aster* that differed in mode of branching were studied by Delisle (42) who concluded from the data "that the branching habit in these species of *Aster* is largely correlated with the amount of auxin produced in the terminal bud and to a lesser extent with that produced in the young leaves".

It was reported by Lehmann (91, 92, 93) that inhibited hybrids of *Epilobium* had less growth substance in the apical bud than normal growing plants, and he suggested that their limited development might be explained on this basis. Heteroauxin was applied to the stem tips of seedlings of *Epilobium* dwarf hybrids (163) and the treatment was observed to cause increased cell elongation and inter-

nodal length, but it decreased the size of developing leaves. Michaelis (118, 120) is vigorously opposed to Lehmann's interpretation that the inhibition phenomenon in crosses between species of *Epilobium* can be explained adequately on the basis of a limiting amount of growth hormone. Went and Thimann (195) have suggested the possibility that sensitivity to growth hormone might be determined by the genes, and auxin production by the cytoplasm.

The facts that there is evidence of inactivation of indoleacetic acid in corollas of *Nicotiana Langsdorffii* (132) and that certain extra chromosomes of this species cause a reduction in flower size (181) has suggested the explanation that these chromosomes may contain genes for small size whose physiological action is to inactivate growth hormone.

The physiology of heterosis is a field which has been actively investigated during the past few years, and a number of papers, both polemical and experimental, have been written on the subject. The work has been confined almost entirely to studies on tomatoes and maize. Whaley (203) has recently reviewed the literature on this phase of heterosis so that no detailed account will be presented here. It is sufficient to say that the only unifying conclusion that can be drawn from the varied but not necessarily contradictory collection of data, appears to be that heterosis involves essentially an increase in growth rate which may take place at any stage of development, with the possible exception of the grand period of growth, from very early (four days after fertilization (39)) to very late (just before maturity (201)), depending upon the genotype under consideration.

The auxin content of maize kernels from plants with varying heterotic vigor has been investigated by Avery and co-workers. They reported that F_1 hybrids were intermediate between their inbred parents in content of growth hormone per gram of endosperm (19) and that there was no apparent relation between the vegetative vigor of hybrids and the amount of auxin stored in the kernels produced by them. It was pointed out, however, that there might be a correlation between auxin content in the vegetative tissue and hybrid vigor, but that research on this problem awaits development of adequate methods for extraction of auxin from green tissues.

Robbins (158, 160) reported that an extract of grains of heterotic hybrid corn produced a greater growth-promoting effect on *Phy-*

comyces than that of either inbred parent. The effect was ascribed to the presence of an unidentified growth-promoting substance called, for convenience, factor *Z* which is present in higher concentrations in the hybrids. It was suggested that the growth of both parents and hybrids may be limited by the quantity of factor *Z* which each synthesizes.

In another paper Robbins (159) reported the results of growing excised roots of two inbred lines of tomato and their heterotic F_1 hybrid in synthetic solution cultures supplemented with various combinations of the growth substances thiamine, pyridoxine (vitamin 6), nicotinamide and thiazole. The F_1 roots grew more rapidly and produced more dry matter than those of either parent except in the solution supplemented with thiazole, in which one parent (Red Currant) grew best. The three kinds of roots responded differently to the different solution cultures and the results were encouraging to the speculation that heterosis might depend on the ability of heterotic plants to synthesize or to utilize growth substances more efficiently than inbred lines.

The study of hereditary differences in the ability of plants to utilize various sources of nutrition offers another method of approach for investigating the physiological basis of size inheritance. There is general recognition of the fact that different species, and to a lesser extent varieties and strains, differ in their response to nutrient conditions, though few investigations have been reported which deal with this matter in any detail.

Harvey (65) grew corn inbred strains and hybrids in aqueous mineral solutions supplied with various nitrogen sources and found that the inbreds showed differential nutritional responses which were attributed to inherent genetic differences in the strains and were transmitted to hybrid offspring. He also grew strains of tomatoes on three deficient nutritional solutions (low N, low P and minus K) and compared the growth with that on a full nutrient solution. Significant differential growth was made by strains on each nutritional deficiency, and the differential response to potassium levels was inherited.

Burkholder and McVeigh (33) observed differential growth of inbred lines and hybrids of maize in response to higher increments of nitrogen which was attributed to differential efficiency in synthesizing protein. Certain soybean varieties from Manchuria when

grown in soil with low available iron showed (194) deficiency symptoms of severe chlorosis, while other varieties under the same conditions made normal growth. This inefficiency in iron utilization was conditioned by a single recessive gene. Aerial tissues of plants homozygous for the inefficient gene had a relatively higher pH, lower soluble iron, higher total iron and lower potassium content than normal. It was suggested that the "gene may condition lower potassium concentration which produces higher pH of cell sap and thereby causes the solubility of iron to be decreased" (194).

It is not unreasonable to conjecture that some of the hereditary differences in size, yield, *etc.*, may be the visible manifestation of gene action which affects physiological processes controlling differential efficiency in the utilization of available nutrition.

The recent work of Beadle and Tatum (23, 188) on *Neurospora* is of particular interest as experimental proof of hereditary differences in growth due to genetically controlled biochemical reactions. Mutant strains, induced by x-rays, were unable to carry out specific biochemical processes essential to the growth of the fungus. In one, the ability to synthesize the thiazole half of the vitamin B_1 molecule was lost; a second was wholly or largely unable to produce vitamin B_6; and in a third strain paraaminobenzoic acid was not synthesized. The latter two strains each differed from normal by a single gene. The deficient strains could be made to grow normally if the missing growth substance was supplied to the culture medium. The results have been summarized (226) as follows: "Mutants so far obtained include strains deficient in the syntheses of the known vitamins, thiamin, thiazole, nicotinic acid, pantothenic acid, paraaminobenzoic acid, and pyridoxin, and the amino acids methionine, lysine, arginine, leucine, and tryptophane. Strains have also been obtained which appear to require certain purines or pyrimidines, but the requirements for these have not been completely worked out as yet".

THE RÔLE OF THE CYTOPLASM IN QUANTITATIVE CHARACTER INHERITANCE

Though the many genes presumably responsible for continuous quantitative variations have not been isolated and studied individually, the bulk of evidence from segregations, similarity of reciprocal hybrids (48), linkages with qualitative characters and effects of

individual chromosomes (see discussion above) should provide adequate grounds for concluding that the factors controlling most hereditary differences capable of experimental analysis are intranuclear, chromosomal and particulate.

Nevertheless, a substantial amount of evidence has been accumulated that the cytoplasm in certain genera plays a differential rôle in heredity (32, 93, 118–120, 134, 151, 197, 222). The characters most liable to be affected by differences in cytoplasmic background are pollen sterility and those of a quantitative nature, as habit of growth and size and shape of vegetative and reproductive organs. The general results have been to demonstrate differences in reciprocal hybrids of such a character that when a certain species or biotype was used as the maternal parent in a cross, and thereby furnished the cytoplasm, the hybrids were inhibited in development, while the reciprocal F_1's were well developed.

It has been concluded, therefore, that certain cytoplasmic substrata exert an influence on hereditary traits which is observed largely as an inhibition of the full expression of particular quantitative characteristics.

In the more recent work of Michaelis (120) he reported results from crossing 38 races of *Epilobium hirsutum* reciprocally with a race from Jena. All crosses with Jena as the male had normal vigor, but in Jena plasma a continuous series of increasing abnormalities was observed in the F_1, depending on the race used as male. Michaelis arbitrarily grouped the hybrids into three classes. The first showed only slight reciprocal differences and the third was very dwarfed and never flowered. The second group of hybrids in Jena plasma were described as dwarfed with reduced leaf size and internode length, various types of leaf spotting, reduced anthocyanin and increased chlorophyll content, reduced flower size and partial or total pollen sterility. The degree of growth inhibition was interpreted as due primarily to the reaction of the genotype of the pollen parent to the inhibiting characteristic of the Jena cytoplasm.

In the F_1 cross of Jena (female) $\times$ München race (male), variants from the normal type of growth inhibition were found, indicating that the München race segregated for genes susceptible to inhibition by the Jena cytoplasm. In the cross of Jena (female) with another race, Wien, the various F_2 and backcross populations indicated the presence of at least three pairs of nuclear genes for

dwarfing, two for abnormal flower size and three for abnormalities of leaf shape. These genes were independent in segregation but acted together in Jena plasma to produce the abnormalities.

The evidence indicates, therefore, that at least in a certain few genera, as *Oenothera* (151), *Streptocarpus* (134) and *Epilobium*, the cytoplasm of one species may inhibit development of the genotype of related species; and, furthermore, that in the latter genus the effect of independent nuclear genes susceptible to plasma-inhibiting influences can be detected.

SUMMARY

Quantitative character inheritance is of interest and importance in genetics, plant breeding and evolution because most characteristics of practical value in agriculture and the majority of differences between species show this type of heredity. According to the generally accepted hypothesis, typical quantitative characters are under the control of a large number of genes or factors which are similar and relatively small in effect, non-dominant in expression, and which act in a cumulative manner. Estimates of the number of genes determining the inheritance of a particular measure of quantity have usually been placed at more than 10 and up to possibly as many as 100 to 200. It is to be expected that, because of the many genes affecting each quantitative character, close linkages would occur which, together with other conditions, would impose severe restrictions on the range of character recombinations in hybrid populations.

The concepts of genes producing manifold effects by controlling primary developmental processes or of a battery of genes determining "genetic coefficients" with either local or general visible manifestation have served to emphasize both additional complexities and possible simplifications in the analysis of quantitative inheritance.

In some experimental material genetic evidence, supported by morphological observations, has shown that gene substitutions affecting size are more nearly geometric than arithmetic in effect. However, a strict and simple geometric interpretation is not compatible with and cannot be expected to apply to all data on size inheritance.

Hybrid vigor or plus heterosis, one type of result in quantitative inheritance, is probably explained best as due to the action of domi-

nant genes favorable for growth which have been accumulated by selection in inbred lines and which in an F_1 are present, in the heterozygous condition, in maximum numbers.

Skewness in the frequency distribution of measurements of quantity may be due to dominance, the nature of gene action, physiological limits to phenotypic expression, interactions of various sorts, and metrical bias. It is difficult to distinguish between these different causes so that caution should be exercised in interpreting the genetic meaning of departures from a normal distribution curve.

A cytogenetic approach to the study of quantitative inheritance is being used increasingly in addition to established and improved methods of statistical analysis. The utilization of inversions and of alterations in chromosome number offer promise for more extensive study in the future.

Developmental investigations on size and shape of plant organs have given us further insight into the more fundamental aspects of their inheritance. It appears that a difference in organ size may be correlated with one in cell size but more often with a difference in number of cells. Similarly, the relation between number of cell divisions and amount of cell expansion in one plane compared to another is the controlling factor in determining differences in shape.

The ultimate physiological or physico-chemical basis for inheritance of any quantitative character is unknown, but clues are suggested by certain recent results demonstrating inherited differences in the production of growth-regulatory substances, in the utilization of plant nutrition, and in the ability to synthesize materials vital to the life processes.

Most genetical studies show that the factors responsible for continuous quantitative variations, while difficult to isolate singly, are nevertheless intranuclear, chromosomal and particulate. Yet there is evidence that in a few genera the cytoplasm plays a differential rôle in heredity by limiting the development of hybrids with certain cytoplasmic substrata. The effect is shown largely by the inhibition of particular quantitative characters.

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dwarfing, two for abnormal flower size and three for abnormalities of leaf shape. These genes were independent in segregation but acted together in Jena plasma to produce the abnormalities.

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